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A COMPARATIVE STUDY OF THE PENES OF THE FAMILY GOMPHIDAE (ORDER ODONATA)

By Lt.-Col. F. C. Fraser, I.M.S. Retd., F.R.E.S.

With Six Plates and One Text-figure.

Manuscript received 8th April, 1940.

(Read 5th June, 1940.)

The primary object of this study was to ascertain if the penile organ offered any characters by which the large number of species included at present in the genus *Gomphus* Leach, could be split up into smaller and more wieldy genera. Needham (1901, *Bull. N.Y. St. Mus.* **47** : 441 and 445) has already carried out such a division and has erected the subgenera *Gomphus* restr., *Stylurus*, *Gomphurus*, *Arigomphus* and *Lanthus* by employing variable complexes of similar characters, which may be venational, shape of abdomen, armature of hind femora in the sexes and the direction of the posterior genital hamules. In practice, however, I find that these characters break down; venational differences appear in the same species and quite often in the opposite wings of a single species; the armature of the hind femora I am quite unable to reconcile, as throughout the Anisoptera, it is the rule that the armature of these limbs differs in the two sexes. The following examples may be cited: *Gomphus fraternus* has only one cell between A1 and A2 and the femoral armature varies in the sexes. *Gomphurus vastus* has the posterior hamule directed strongly posteriorwards, not perpendicular to abdomen, and the femoral armature varies in the sexes. *Stylurus plagiatus* has the posterior hamules directed posteriorly, not forwards, and the femoral armature again varies in the sexes. *Arigomphus spicatus* has the venation very variable and often only one cell between A1 and A2, and this variation may be found in the opposite wings of a single specimen. It may be said here, at the outset, that the structure of the penes in these subgenera does not warrant their separation from the genus *Gomphus* sens. str.

The family Gomphidae has offered difficulty in classification probably to a greater extent than any other family in the order Odonata, consisting, as it does, of a large number of species all closely similar in their colouring and general facies. Williamson introduced a valuable means of splitting up the family, when he pointed out the great variation in the number of cross-veins between the veins Rs and MA in the hind-wings, and this feature has since been employed by Laidlaw and myself to form the two subfamilies Gomphinae and Epigomphinae, the former having not more than 2 cross-veins between Rs and MA, the latter having more than 2. Here again, however, the structure of the penes in genera belonging to the two subfamilies is found, in some cases, to be the same, or, in other words, the penes, in some cases, are found to be more homogeneous than the venation. Such a finding was totally unexpected and extremely disconcerting. Another disconcerting fact has also come out during this study, and that is the finding of totally different types of penes in species which had every appearance of belonging to a single genus (*Ictino-*

gomphus and *Anisogomphus*). One is thus placed on the horns of a dilemma, whether to accept the evidence of venational or penile characters, when the two are totally at variance. In the case of *Ictinogomphus* I have already accepted the evidence of the penis as necessitating a splitting of the genus into smaller genera, but here it is possible to find other characters to support such a step; in the case of *Anisogomphus* I have not been able to do so, and have preferred to let the genus stand as it is at present, treating the variations of the penes as specific characters, although, it must be confessed, with considerable doubt.

The penis of the Gomphidae, as in all the Anisoptera, consists of three segments and a vesicle, which latter, according to Tillyard, serves for the storage of the sperm-capsules. He does not state that he has actually found the sperm-capsules in the vesicle, nor do I know of any investigator who has found this to be so; certainly I have never been able to find them in this receptacle. Of the Zygoptera, where a vesicle rarely exists, Tillyard states that the penis is a blind organ and that the sperm-capsules are deposited by the female in the genital fossa. I believe that the penis is also blind in the Anisoptera and that the same process is performed by the female. The vesicle appears to be, first, an erective organ with its cavity continuous with that of the penis and attached to the latter by a membranous ginglymus joint. When pressure is raised in the vesicle, the membranous joint is distended and the penis at once erected; in other words, the mechanism is exactly similar to that by which the Odonate larva throws out its labial mask when seizing its prey. The function of this pseudo-penis, both in the Anisoptera and Zygoptera, appears to be no more than a swab to transfer the sperm-capsules from the genital fossa to the female vagina. The second function of the vesicle is to protect the delicate flagellae which are usually found at the apex of the penis, and which, when at rest, lie snugly in the deep groove between the two lips on the fore part of the vesicle. The first joint of the penis, which I call the *stem*, is stout and usually somewhat C-shaped; it is covered dorsally by a narrow grooved sheath, which Tillyard has described as a protective organ for the penis when at rest. I am not altogether of this opinion and, from the shape of the organ, believe that it is purely a " director " in function, serving to steady and give a straight thrust to the penis when the latter is functioning. The second joint is also stout and highly chitinised on its dorsum, and usually shorter than the first segment; its function is probably to give greater mobility to the penis and possibly it serves also as a release valve, permitting the penis to collapse and be withdrawn; the tiny aperture on its upper surface suggests such a mechanism. The third or apical segment is the *glans* and is partly chitinous, partly membranous, and usually furnished with two, more or less elongated, curled or curved flagellae. Beneath it, in many species, projects a spoon-like organ, the prepuce, the function of which is unknown, but which may serve as a scoop, to spoon up the sperm-capsules from the genital fossa.

I have been able to figure some 84 penes belonging to 53 genera and have examined a great number of others belonging to the genera of which examples have been figured. Specific differences are frequent and often wide, so that, for some genera, I have been compelled to show more than one example. For material, I have relied largely on my own collections, but for others I am indebted to the authorities of the British, Paris, Vienna and Genoa Museums; all figures have been made by myself by means of the camera lucida, except that of *Libyogomphus tenaculatus* (figs. A and B), which was drawn by Mr. D. E. Kimmins of the British Museum. The late Mr. Kenneth Morton and

Dr. Laidlaw kindly loaned me several specimens, which are figured and described here, and to all these collaborators, I owe my thanks. Dr. Clarence Kennedy loaned me his single specimen of *Archaeogomphus hamatus*, and with this exception I met with a blank refusal of help from all American institutions. This attitude of regarding specimens of dollar, rather than of scientific, value, is greatly to be deplored and is equivalent to raising tariff barriers to the spread of science. Thus the work of reporting on material in American collections must be done at some future date by American students who may be better favoured than I have been.

The most frequent form of penis is that typified by *Gomphus vulgatissimus* (Linn.) and *G. postocularis* Selys, the two species having the organ practically similar, even to the vesicle which is notoriously variable in shape. In them, the latter is large and basin-shaped, and roughly cordate in a profile outline, the lip is rounded and fissured more or less deeply at its middle, this fissure being prolonged inwards to afford a receptacle for the glans; the *stem* is short and thick and usually of the same length as the *middle segment*, which latter is cylindrical at its base and somewhat expanded apically, especially below where is often found a bulky preputial fold extending forward beneath the glans and shaped somewhat like a spoon. The *glans* is of moderate size, shaped rather like the flower of an arum and with its lower apical end produced as a curved or curled flagellum which is usually composed of two closely apposed filaments. This type of penis is found in the following genera: *Gomphus* Leach, *Gomphurus* Need., *Lanthus* Need., *Arigomphus* Need., *Stylurus* Need., and *Dromogomphus* Selys of the subfamily GOMPHINAE, and *Macrogomphus* Selys of the subfamily EPIGOMPHINAE; in the two last genera, the flagellum is spirally curled at its apex. The vesicle of this large complex shows considerable variety in shape as will be seen by referring to pl. 1, figs. 1–8, and, in *G. agricola* Ris, the lip has a robust cone-shaped process on each side anteriorly. The glans is variable within limits, being very minute in *G. agricola* and produced enormously in *G. exilis* Selys, *G. lineatifrons* Calv., and *G. vastus* Walsh.

In *Microgomphus* of the EPIGOMPHINAE, a somewhat similar type of penis exists but the middle segment is shorter than the stem and the glans elongated, tubular and with the arum-like apex inverted and the filaments of the flagellum divaricate (pl. 1, fig. 9).

The next common type of penis is found in the genus *Onychogomphus* Selys. The vesicle is usually jug-shaped but is again extremely variable in form: in *O. aureus* Laid., two conical processes are found on the lips, very similar to those found in *G. agricola* but more closely apposed: in *O. flexuosus* and *O. forcipatus* these are replaced by short robust spines; the stem is club-shaped, gradually thickening apically, where, on the dorsal surface, is found quite commonly a robust obtuse spine; the middle segment is nearly always shorter than the stem and its prepuce is poorly developed and often situated near the base, and, in some cases, reflected on to the stem where it forms a prominent spine (pl. 2, fig. 2). The glans is very characteristic, the basal portion is usually prolonged as a tubular structure, from the apex of which arise long sharply turned down flagellae, the whole structure presenting a claw-like appearance. Variations of this type among the species are considerable and are best gathered by a reference to the figures (pl. 1, figs. 10–13; pl. 2, figs. 1 and 2, 5 and 6). *O. pulcherrimus* Fraser differs from the rest by the glans not bifurcate at apex and the flagellae longer and directed forwards and upwards as in *Paragomphus*, to which genus this species may actually belong. It is an aberrant one, especially in its colouring, which has no counterpart in the rest of the family.

O. schmidti Fraser and *O. bistrigatus* Selys, although otherwise typical of the genus, have the penes, which are similar in both, entirely different from any others in the genus; the glans is narrowly tubular, with a frilled border at its apex and without any evidence of flagellae. A long, narrow, prominent preputial fold extends from the base of the middle segment ventrally, well towards the apex of glans (pl. 2, figs. 3 and 4). *O. circularis* Selys is another aberrant form with anal appendages quite different from others in the genus, but with typical venational details; the penis differs from all others and is characterised by two small processes projecting forwards from the apex of the medial segment which are reminiscent of the eyes of a snail; the glans is very bulky, produced anteriorly and furnished at the apex with a pair of very small and stunted flagellae.

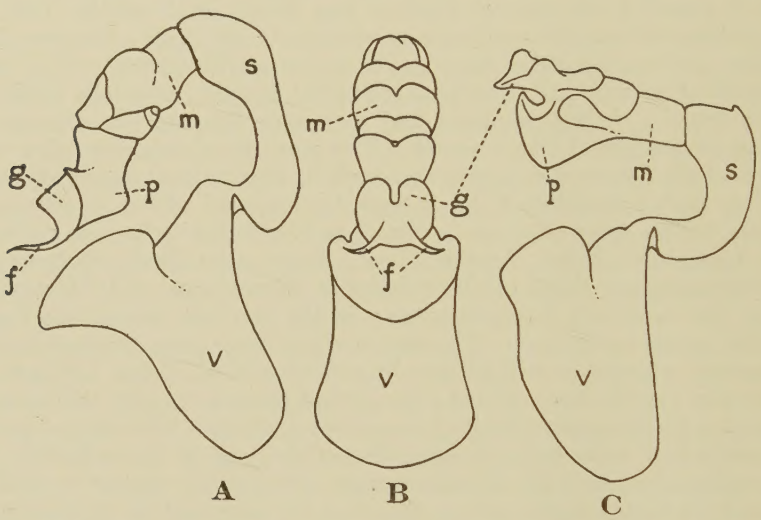


Fig. 1.—A and B. Left lateral and dorsal views of the penis of *Libyogomphus tenaculatus* Fraser; C. left lateral view of the penis of *Stylogomphus inglisi* Fraser. *V*, vesicle; *S*, stem; *m*, median segment; *p*, preputial fold or prepuce; *g*, glans; *f*, flagellum.

Closely similar to the Onychogomphine type of penis, as might be expected, is that of *Paragomphus* Cowley (pl. 2, figs. 8–10), in which the glans is very similar but has the flagellae longer and curling upwards like the tusks of an elephant.

Libyogomphus Fraser (figs. A and B) has also a penis of the *Paragomphus* type and, as it has other characters which seem to relate it to the *Onychogomphus*-complex, it is clearly related to this genus.

Erpetogomphus Selys, a genus which parallels *Paragomphus* in the New World, has the penis of very similar formation and suggests that it has arisen from the Old World complex of *Onychogomphus* (pl. 5, fig. 7; pl. 6, fig. 13). *Lamelligomphus* Fraser, which formerly formed part of genus *Onychogomphus*, differs widely in the structure of its penis from that genus and thus justifies its separation. There is a large preputial fold beneath the median segment exactly similar to that found in *Gomphus* and the glans has the flagellae of great length and with their bases greatly dilated as lateral flaps to the glans. *Lestinogomphus* Martin (pl. 2, fig. 11), and *Ceratogomphus* Selys (Ethiopian

genera) (pl. 2, fig. 12) are closely related to *Paragomphus*; in the former, the glans is withdrawn into the apex of the median segment and the flagellae are short and broad of base; in the latter, the glans is petiolated, the free border is markedly frilled, the flagellae are of the long, watch-spring type and each is split to its base, so as to form four long whip-like filaments. *Crenigomphus* Selys (pl. 3, figs. 4 and 5; pl. 5, fig. 11), which is also closely related to *Onychogomphus*, has the glans frilled as in *Ceratogomphus*, flagellae of considerable or moderate length or obtuse and curled at apex, and a very robust ventral spine to the medial segment (a second more anterior and smaller spine is found in *C. hartmanni* Forst.). *Podogomphus* Karsch (pl. 3, fig. 6) and *Notogomphus* Selys (pl. 4, fig. 15) have been amalgamated by Miss Longfield (1936, *Trans. R. ent. Soc. Lond.* **85** : 478) but the structure of the penes does not support this. That of the former is entirely without any flagellae and has a ventral spine beneath the medial segment as in *Crenigomphus*. In *Notogomphus* this ventral spine is entirely lacking and the glans is very small and almost entirely concealed beneath a hood-like fold very similar to that found in *Leptogomphus bidentatus* Fras. (pl. 4, fig. 11). With such existing differences, I would prefer to preserve the two genera apart.

Lastly, the remaining African genus *Oxygomphus* Martin (pl. 3, fig. 10) appears from the close similarity of its penis to lie close to genus *Gomphus*.

The Oriental genera, which also include the Ethiopian *Paragomphus*, are largely monotypic and their penes are more often unique in structure. *Megalogomphus* Campion lies near *Gomphus*, but has the preputial fold long and attenuated and simulating a robust ventral spine; the glans is widely splayed at its orifice of which the lateral borders are foliate and frilled, whilst the flagellae sweep upwards in an abrupt curve, becoming divaricate as they do so. *Merogomphus* Will., which contains four very doubtfully related species, exhibits penes so entirely variable as to support this contention (pl. 3, figs. 1–3). In *M. longistigma* (Fraser) the glans is beautifully frilled, with borders everted, and the short, thin flagellae are directed laterally from its upper edge; *M. martini* (Fraser) has the flagellae arising from the lower border and broadly lobate at base, whilst *M. paviei* (Martin), the genotype, has no flagellae at all!

Burmagomphus Will., which Needham merged with *Gomphus* (1930, *Zool. Sinica* (A) **11** : 46), is, in my opinion, a well-defined genus, and the structure of the penis supports this (pl. 3, fig. 9). It is one of the most highly specialised organs found in the family and the bulbous glans with its enormously elongated, whip-like flagellae is entirely without counterpart among the genera. During rest, the flagellae are folded on themselves beneath the median segment of the penis.

Davidioides Fraser (pl. 3, fig. 8) is another genus difficult to place and its uniquely formed penis offers no assistance in this. The medial segment has a spine-like preputial fold and an unique castellated structure perched on the dorsum of its apex; the glans is large, trumpet-shaped, with a frilled border and an obtuse basal ventral spine.

Cyclogomphus Selys (pl. 3, fig. 7) is characterised by its enormous gourd-like vesicle, which is paralleled only in *Nepogomphus* Fraser, in which, however, it is egg-shaped. The stem is extremely short and quite straight; the glans is very simple and represented by a small, triangular process bifurcated at the apex. In *Nepogomphus*, which formerly formed part of the major genus *Onychogomphus*, the stem is short and sharply angulated; the middle segment is longer and furnished dorsally at its apex with two divaricate, robust spines which overhang the base of the glans; the glans has two short, markedly curled,

divaricate broad flagellae. This penis is unique in structure and difficult to compare with any others in the family (pl. 4, fig. 12).

Acrogomphus Laidlaw and *Ophiogomphus* Selys may be considered together, as their penes are remarkably similar in structure, although the two genera do not appear to be otherwise closely related (pl. 4, figs. 5 and 4). In them the preputial fold is well developed and spine-like in profile; the glans is backed by a bilobate ruff-like collar and the apex is produced into two long flagellae curling upwards like the horns of a bull; above and between them is found a large downwardly turned spine which arises from the dorsum of the glans. The whole structure is so intricate in design, that it is difficult to conceive that they represent an example of parallel development, yet this must be the case as other generic characters show no close relationship.

Platygomphus Selys shows a structure of the penis which approaches that of *Lamelligomphus*; the preputial fold is similar but the flagellae of the glans are ribbon-shaped and spirally twisted; it is clearly a modification of the *Gomphus*-type (pl. 4, fig. 13).

Heliogomphus Laidlaw (pl. 4, figs. 6–8) possesses a penis of the *Gomphus*-type, but slightly modified. The preputial fold is very bulky; the glans very small and inconspicuous and with a frilled border. *Stylogomphus* Fraser, which presents some of the characters of *Heliogomphus* in its anal appendages, also agrees with that genus in the structure of its penis; the glans is, however, of larger dimensions. Venationally *Stylogomphus* belongs to the subfamily Gomphinae, whilst *Heliogomphus* belongs to the Epigomphinae, so that here again, as in the case of *Macrogomphus*, one finds the present classification breaking down (fig. C). *Leptogomphus* Selys (pl. 4, figs. 9 and 10), of the subfamily Epigomphinae, has been regarded as closely allied to *Heliogomphus*, but the shape of the penis is very different; the median segment shows a broad convex ventral expansion which may represent the prepuce; the glans is very deep and bulbous, with more or less elongated flagellae curling out from each side. *Leptogomphus bidentatus* Fraser, which I find by a fresh examination of the venation, does not belong to the subfamily Epigomphinae, and so cannot belong to the genus *Leptogomphus*, possesses a penis closely similar to that of *Heliogomphus*, although it clearly does not belong to this genus. The preputial fold is very similar to that of *Gomphus*; the glans, which is very small, is almost entirely concealed beneath a hood-like fold which envelops it from above and laterally (pl. 4, fig. 11). The position of this species is doubtful and as it does not belong to any described genus a new one is necessary to accommodate it (see Appendix, p. 549).

Davidius Selys (pl. 4, fig. 14) possesses a penis similar to that of *Heliogomphus* and *Stylogomphus*. Its simple nature and build is but a modification of the *Gomphus* type, belonging to the same subfamily, and it approaches *Gomphus melampus* Selys most nearly. The latter is somewhat aberrant in its genus, as also is *Gomphus suzukii* Oguma, whose penis is exactly similar to that of *melampus*; the description of these two species tallies so closely that I think there is no doubt that they are synonymous. They probably represent an intermediate form between *Gomphus* and *Davidius* (**syn. n.**).

Anisogomphus Selys (pl. 4, figs. 1–3) contains three species in which the penes differ widely in all details. Those of *A. occipitalis* (Selys) and *A. bivittatus* (Selys) appear to be broad modifications of the *Gomphus* type, with broad, spoon-like preputial folds extending forwards beneath the glans, the latter being narrowly tubular and elongate and entirely without flagellae; in the former, the great length of the medial segment and glans is accommodated

by a complementary lengthening of the anterior lip of the vesicle. That of *A. orites* Laidlaw has the prepuce shaped as a large conical spine, and the glans, an enormously expanded copy of that of *Gomphus*.

Perissogomphus Laidlaw (pl. 5, fig. 4) has a massively built penis with the stem expanding broadly towards its apex and the glans of great size with its upper border overhanging hood-like, and the lower border produced downwards and then upwards in a broad curve, ending finally in two long divaricate flagellae. It is a unique type of penis, as would be expected in so aberrant a genus, but it suggests a derivation from *Ophiogomphus*.

Hagenius Selys and *Sieboldius* Selys (pl. 3, figs. 12 and 13) have similar shaped penes; very little separates these two genera. The vesicle is deep and barrel-shaped; the glans small and out of all proportion to the rest of the penis; its borders are markedly frilled and it is without flagellae. Its structure offers no key to the relationships of the genera.

Isomma Selys (pl. 5, fig. 9). This genus, confined to Madagascar, has the vesicle of the penis with anterior border greatly produced to accommodate the elongated glans, which is of simple tubular design and with a long bifurcated flagellum issuing from its lower border; the stem is excessively curled and the median segment is produced below at its apex although not in the form of a preputial fold. The structure of the organ gives no clue to the relationships of the genus.

Archaeogomphus Will. (pl. 3, fig. 11) possesses a penis of unique formation characterised by the presence of two closely apposed dorso-apical horns on the median segment; the vesicle is proportionately very small; the glans is funnel-shaped with markedly frilled borders, this frill prolonged along the upper borders of the flagellae; the latter are broad at base, of great length, curled strongly and divaricate. Beneath it, expands a *Gomphus*-like preputial fold: the only point of resemblance to this genus. Its complicated structure serves to emphasise the isolation of *Archaeogomphus*.

Austrogomphus Selys (pl. 5, figs. 12 and 13). Species belonging to the genus possess penes of close similarity in structure and of such complicated and unique shape as to point to a long isolation of the genus. The middle segment is generally longer than the stem and is furnished with a long, under-slung, narrow, spatulate-like prepuce, which is spined above in some species; the apical dorsal angles are produced forwards to form a horseshoe-shaped collar, which is narrow or obtusely dilated as lateral flaps; these two arms embrace the glans which rises up in the recess formed by them; the glans is trombone-shaped, with a tubular stem which at first curves down and then abruptly upwards again, finally ending in a large trumpet-like orifice, the anterior lower lip of which is prolonged into a very long bifid flagellum; from its sides, two ungulate processes rise up between the fork of the horseshoe collar.

Neogomphus Selys (pl. 5, fig. 3) has the median segment much shorter than the stem and a glans as long as the first two segments taken together; this latter is narrowly cylindrical, curved strongly downwards and deeply bifid at its apex from which arise two long ribbon-like flagellae. The anterior lip of the vesicle is produced to accommodate the extended glans.

Epigomphus Selys (pl. 5, fig. 8) belongs to the *Gomphus*-type; the median segment is produced apically and the glans, shaped as in *Gomphus*, is suspended from below its bevelled end. There is a preputial fold arising from the end of the median segment, also as in *Gomphus*, but the flagellum is of much greater length than in that genus.

The remaining genera which I have been able to examine all belong to the

subfamily Ictinogomphinae: *Ictinogomphus* Cowley (pl. 6, fig. 1) and its allies are characterised by the great length of the first two segments of the penis and the total absence of the preputial fold. In the present genus, the stem gradually thickens apically and is of the same length as the median segment; the glans is of intricate design with its upper basal corners projected forwards as two robust spines, and there is a third spine projecting backwards from the middle of its ventral surface; there are no flagellae. *Indictinogomphus* Fraser (pl. 6, fig. 2) has the first two segments similar to the last genus but the median segment is dilated below into a sort of membranous keel; the glans is deeply cleft transversely into upper and lower lips, the lower of which projects beyond the upper, and from its sides, near the base of the cleft, tusk-like spines are given off and project obliquely forwards and upwards. *Sinictinogomphus* Fraser (pl. 6, fig. 3) has the stem longer and rather sinuous; the median segment is only half the length of the stem and expands at its apex; the glans is of remarkable shape, enormously long and expanded at its apex, then again tapering, to end in two short, strongly curled flagellae. *Austrictinogomphus* gen. n. (pl. 6, fig. 4) (p. 550). This new genus is erected to contain *Ictinus acutus* Laid., a very aberrant species, which differs not only in the shape of its male anal appendages but is found to possess a very different type of penis from those of other species (see Appendix for definition of genus). The penis has a vesicle closely similar to that of *Ictinogomphus* and the stem is of the same great length, but the median segment is shortened to two-thirds the length of stem; the glans is dilated laterally at its base and is then narrowly tubular to the apex which expands as two ear-shaped flaps, from between which, below, projects a short tongue-like process. *Gomphidia* Selys (pl. 6, figs. 8 and 9) has the penis very similar to *Ictinogomphus* save for the glans which possesses a short medial tubular stem, on each side of which flagellae of enormous length extend forwards; these are rather broad at base but gradually taper away to a thread-like thickness, the ends being curled in two or three watch-spring spirals. *Lindenia* Selys (pl. 6, fig. 10) has a vesicle similar to *Ictinogomphus* but the stem is shorter and stouter; the median segment is of the same length, somewhat tubular and expanding rather abruptly at apex; the glans is short and shaped like a sugar-scoop and is without flagellae. *Cacus* Selys (pl. 6, fig. 12) possesses two specific types of penis but it is possible that Needham's species, *C. mungo*, belongs to a new genus. That of *C. latro* Erich. has a vesicle like that of *Ictinogomphus*; the stem is robust, but slightly curved and thickened apically; the median segment is of the same length and subtubular in shape; the glans is flat and spatulate and very obtuse at apex; its sides curl up like the leaf of a *Nepenthe* to form a shallow cup above, through the longitudinal diameter of which is a raised membranous ridge; flagellae are absent. That of *C. mungo* is an exact replica of that of *Lindenia*, which fact may indicate an origin of the American forms of this group from the Ethiopian!

Phyllogomphus Selys (pl. 6, fig. 7), which is more distantly related, has the apex of the vesicle greatly produced; the stem is of stouter build than in former genera; the median segment is sinuous, tubular and longer than the stem; the glans is rather simple and small in scale; its lower border is produced as a pseudo-preputial fold and from above this, projects a long bifid flagellum, the two filaments of great length and thread-like.

Progomphus Selys (pl. 5, figs. 1 and 2). Species belonging to this genus possess highly characteristic and specialised penes; the median segment is very short and has a robust spine, often of great length, projecting from its base ventrally and forwards, which may represent the prepuce; the glans is

narrowly elongate and resembles *Gomphidia* by having two enormously lengthened, tapering watch-spring flagellae; specific differences are noticed in the shape and length of the ventral spine and flagellae.

Cyclophylla Selys (pl. 5, fig. 6). The stem is rather short and with an obtuse apical, dorsal spine; the median segment is extremely short and is deficient of prepuce or ventral spines; the glans is broadly funnel-shaped, with its lower apical border produced into a long watch-spring-like flagellum which splits into two filaments. *Aphylla* Selys (pl. 6, fig. 11) has the stem short and straight, broadened at apex, which is furnished dorsally with an obtuse spine; the median segment is of the same length as stem; the glans is shortly tubular with an elongated narrow fold on each side which ends in a very short process representing a degraded flagellum. *Gomphoides* Selys (pl. 6, figs. 5 and 6). The penis is very characteristic and differs widely from that of *Aphylla*, which genus has been regarded of late years as synonymous to *Gomphoides*. Needham, in a recent paper (1940, *Trans. Amer. ent. Soc.* **65** : 363), maintains that the two genera are distinct and the formation of the penis, as found here, tends to support this view. The vesicle has the lip produced squarely as seen in profile, and its upper part is conically elongated; the median segment is almost suppressed and not more than one-fourth the length of stem; the glans is tubular with upper and lower borders frilled and produced; a long narrow flagellum, which is bifid for most of its length, springs from the floor of the glans and is directed in a gentle upward and forwards curve. Lastly *Zonophora* Selys (pl. 5, fig. 10), which appears to be related to the last by the shape of its penis, has an extremely abbreviated median segment and a long tubular glans from which a very elongated bifid flagellum projects.

To summarise, I am of opinion that the taxonomic value of the characters of the penes of the Gomphidae is largely doubtful. In many cases, these characters are merely specific, in others, they are of undoubted generic value, and in still others, they tend to throw doubt on the present position of species within genera and of genera within subfamilies. Generally, it would be unwise to place too much value on, or to rely solely on, these characters for placing any particular species or genus. In the case of the splitting up of the *Ictinogomphus*-complex, I have supported the characters of the penes by others such as those of venation etc., and this should be the correct practice to adopt in the case of the Gomphidae.

Appendix.

Dubitogomphus gen. n.

This new genus is raised to accommodate a single aberrant species of Gomphine : *Leptogomphus bidentatus* Fraser (1930, *J. Bombay nat. Hist. Soc.* **34** : 752). A re-examination of the venation shows that it actually belongs to the subfamily Gomphinae and not to the Epigomphinae, so that it cannot belong to genus *Leptogomphus*. Attention to this fact was directed by finding that the penis did not conform to the *Leptogomphus* type. The definition of the new genus is as follows :—

Dragonflies belonging to the subfamily Gomphinae of the Gomphidae, of large size and melanotic colouring; occiput of female armed with two robust spines; anal appendages of *Leptogomphus* type; wings tinted with yellow at base; discoidal cells of hind-wings traversed by a cross-nervure; anal-loop absent; no incomplete basal antenodal vein

present; 2 rows of cells in anal field of fore-wing, 6 rows in the hind-wing; a short accessory vein to the discoidal cell often present; anal vein, in both wings, markedly pectinate; reticulation very close. Breeds in still waters.

Genotype : *Leptogomphus bidentatus* Fraser.

The position of this genus is not clear but it appears to lie near the aberrant genus *Perissogomphus* Laidlaw. (The characters of the penis are given above, and are therefore not repeated in the generic diagnosis.)

Austrictinogomphus gen. n.

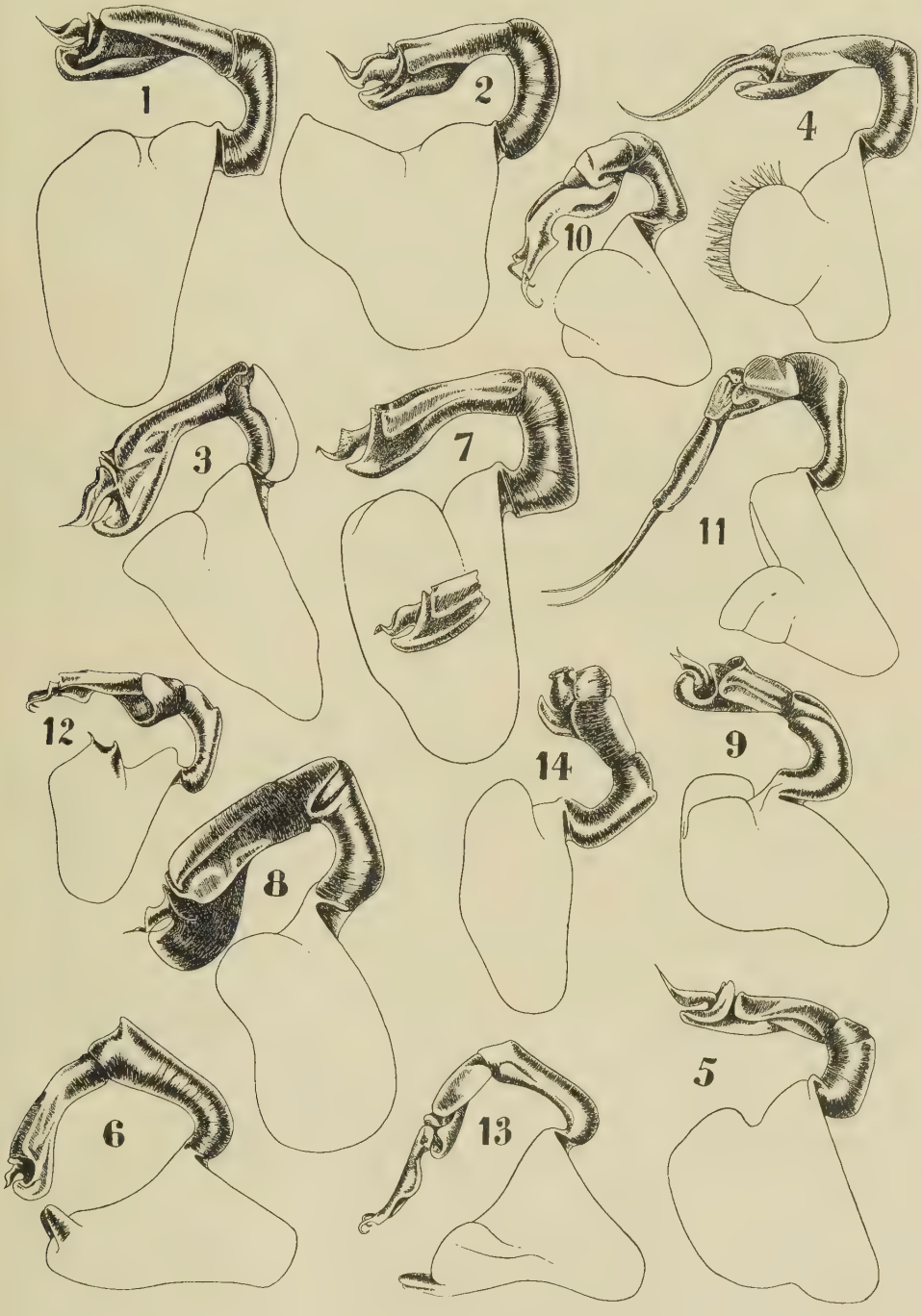
(The following generic diagnosis should be read in conjunction with those for *Ictinogomphus*, *Indictinogomphus* and *Sinictinogomphus* which appeared in 1939, *Proc. R. ent. Soc. Lond.* (B) **8** : 21.)

A genus of less robust species; subtriangle made up of 3 cells; discoidal field with only 2 rows of cells; anal-loop made up of 5 cells; tornal angle slightly produced, its sides enclosing a slightly acute angle; lateral borders of segment 8 moderately dilated; penis (as described above).

Genotype : *Ictinus acutus* Laidlaw. Distribution Papuan.

Explanation of Plate 1.

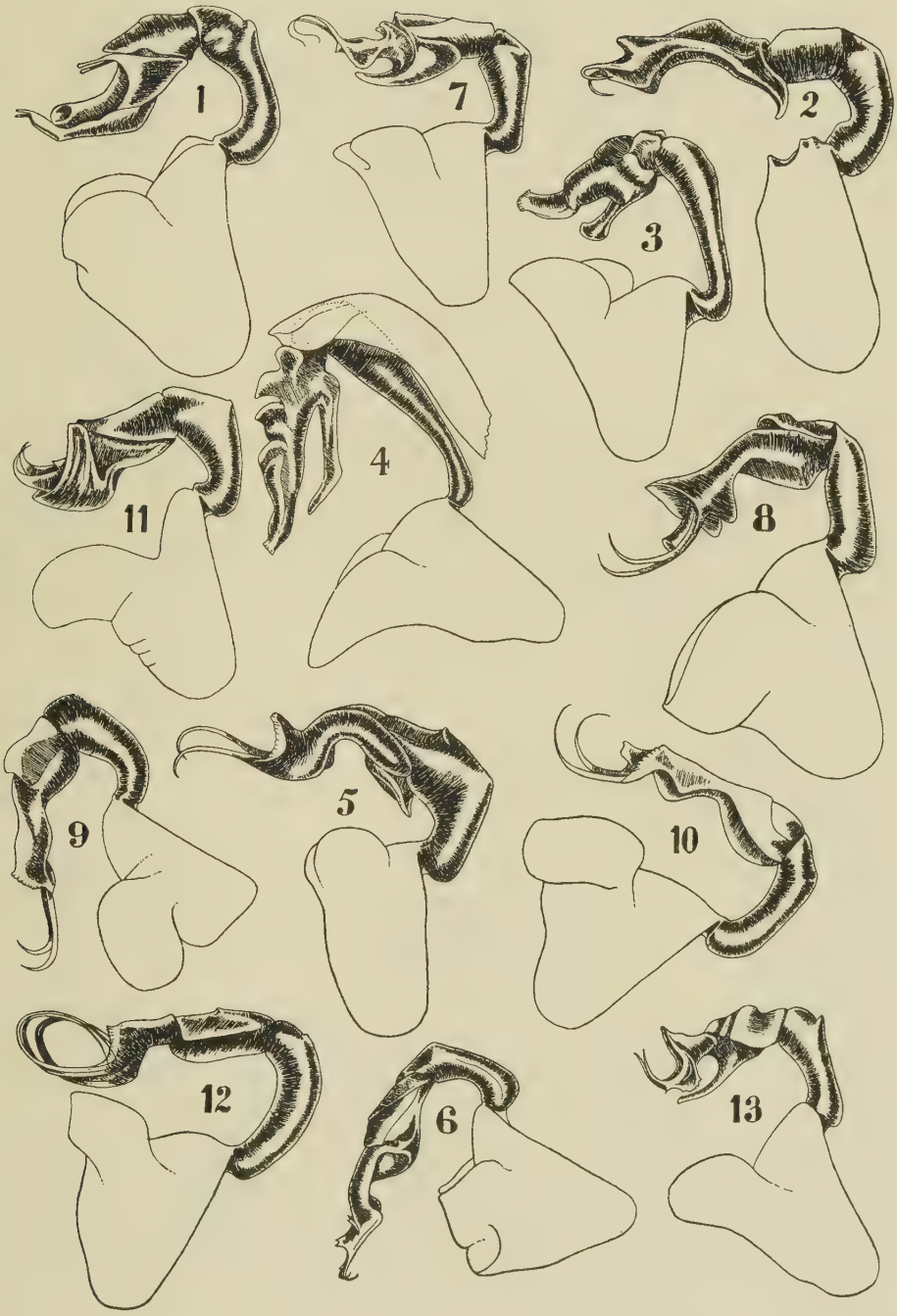
Penile organs of : 1. *Gomphus abdominalis* McLach.; 2. *Gomphus vulgatissimus* (Linn.); 3. *Gomphus melaenops* Selys; 4. *Gomphus exilis* Selys; 5. *Gomphus minutus* Rambur; 6. *Gomphus agricola* Ris; 7. *Dromogomphus spoliatus* (Selys), inset, apex of penis of *Dromogomphus spinosus* (Selys); 8. *Macrogomphus annulatus* (Selys); 9. *Microgomphus torquatus* Selys; 10. *Onychogomphus duaricus* Fraser; 11. *Onychogomphus pulcherrimus* Fraser; 12. *Onychogomphus flexuosus* (Schneid.); 13. *Onychogomphus aureus* Laid.; 14. *Gomphus suzukii* Oguma (= *Gomphus melampus* Selys).



Fraser: Study of the penes of GOMPHIDAE.

Explanation of Plate 2.

Penile organs of: 1. *Onychogomphus circularis* Selys; 2. *Onychogomphus forcipatus* (Linn.); 3. *Onychogomphus schmidti* Fraser; 4. *Onychogomphus bistrigatus* Selys; 5. *Onychogomphus uncatus* (Charp.); 6. *Onychogomphus saundersii* Selys; 7. *Lamelligomphus nilgiriensis* (Fraser); 8. *Paragomphus lindgreni* (Fraser); 9. *Paragomphus cognatus* (Rambur); 10. *Paragomphus lineatus* (Selys); 11. *Lestinogomphus africanus* (Fraser); 12. *Ceratogomphus pictus* Selys; 13. *Megalogomphus hannyngtoni* Fraser.



Fraser: Study of the penes of GOMPHIDAE.

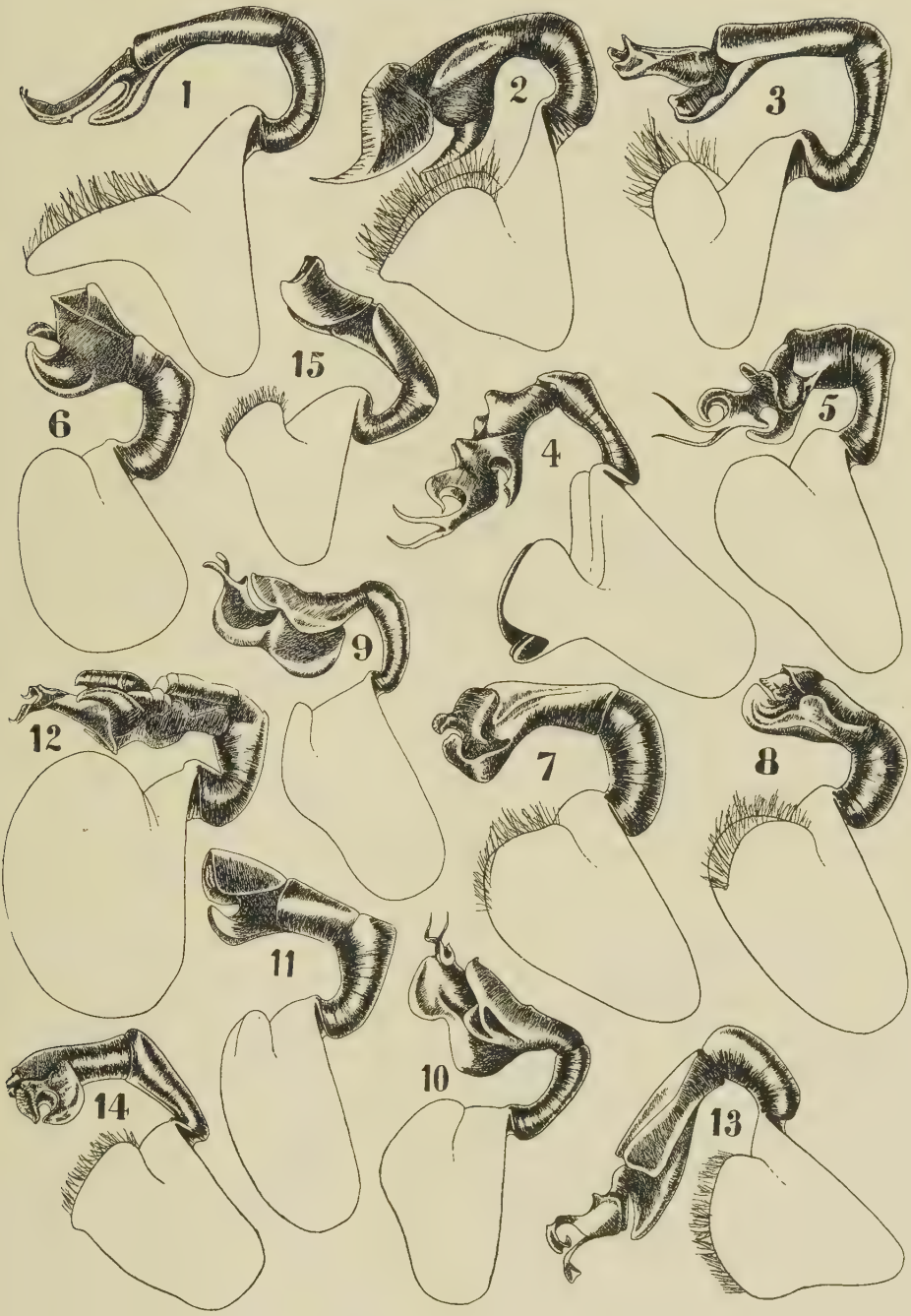
Explanation of Plate 3.

Penile organs of: 1. *Merogomphus longistigma* (Fraser); 2. *Merogomphus paviei* Martin; 3. *Merogomphus martini* (Fraser); 4. *Crenigomphus hartmanni* Forster; 5. *Crenigomphus abyssinicus* Selys; 6. *Podogomphus leroyi* Schouten.; 7. *Cyclogomphus ypsilon* Selys; 8. *Davidioides martini* Fraser; 9. *Burmagomphus pyramidalis* Laidlaw; 10. *Oxygomphus agilis* Martin; 11. *Archaeogomphus hamatus* Will.; 12. *Hagenius brevistylus* Selys; 13. *Sieboldius nigricolor* (Fraser).

Fraser: Study of the penes of GOMPHIDAE.

Explanation of Plate 4.

Penile organs of: 1. *Anisogomphus occipitalis* (Selys); 2. *Anisogomphus orites* Laidlaw; 3. *Anisogomphus bivittatus* (Selys); 4. *Ophiogomphus reductus* Calvert; 5. *Acrogomphus fraseri* Laidlaw; 6. *Heliogomphus retroflexus* (Ris); 7. *Heliogomphus promelas* (Selys); 8. *Heliogomphus drescheri* Lieftinck; 9. *Leptogomphus lansbergei* Selys; 10. *Leptogomphus gestroi* Selys; 11. *Leptogomphus bidentatus* Fraser; 12. *Nepogomphus modestus* (Selys); 13. *Platygomphus dolabratus* Selys; 14. *Davidius aberrans* Selys; 15. *Notogomphus dorsalis* (Selys).



Fraser: Study of the penes of GOMPHIDAE.

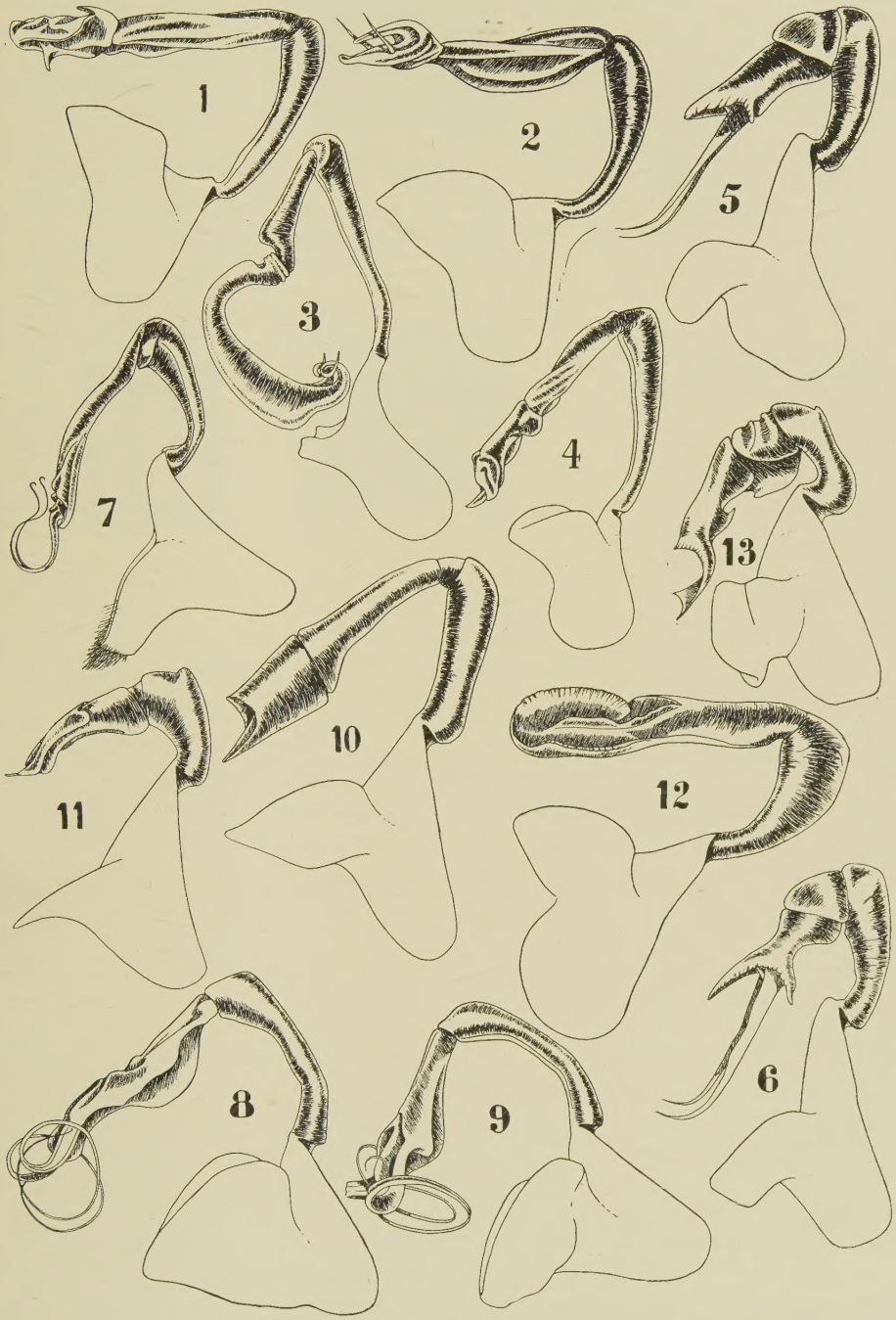
Explanation of Plate 5.

Penile organs of: 1. *Progomphus borealis* Selys; 2. *Progomphus pygmaeus* Selys; 3. *Neogomphus molestus* (Selys); 4. *Perissogomphus stevensi* Laidlaw; 5. *Anormogomphus kiritschenkoi* Bartenef; 6. *Cyclophylla signata* Selys; 7. *Erpetogomphus compositus* Selys; 8. *Epigomphus llama* Calvert; 9. *Isomma hieroglyphicum* Selys; 10. *Zonophora campanulata* (Burm.); 11. *Crenigomphus renei* Fraser; 12. *Austrogomphus ochraceus* Selys; 13. *Austrogomphus collaris* Selys.

Fraser: Study of the penes of GOMPHIDAE.

Explanation of Plate 6.

Penile organs of: 1. *Ictinogomphus ferox* (Rambur); 2. *Indictinogomphus rapax* (Rambur); 3. *Sinictinogomphus clavatus* (Fabr.); 4. *Austrictinogomphus acutus* (Laidlaw); 5. *Gomphoides semicircularis* Selys; 6. *Gomphoides calverti* Will.; 7. *Phyllogomphus aethiops* Selys; 8. *Gomphidia t-nigrum* Selys; 9. *Gomphidia fletcheri* Fraser; 10. *Lindenia tetraphylla* (Van der Lind.); 11. *Aphylla producta* Selys; 12. *Cacus latro* (Erichs.); 13. *Erpetogomphus natrix* Will.



Fraser: Study of the penes of GOMPHIDAE.